
Generic Evaluation of *Boleum*, *Euzomodendron*, and *Vella* (Brassicaceae)

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ABSTRACT. Morphological, cytological, and molecular data support the reduction of *Boleum* Desvaux and *Euzomodendron* Cosson to synonymy of *Vella* L. The new combination *Vella bourgaeana* is proposed. A key to the species of *Vella* is presented.

Boleum and *Euzomodendron* have generally been recognized as monotypic Spanish genera, and *B. asperum* (Persoon) Desvaux was originally described as *Vella aspera* Persoon. *Vella*, on the other hand, includes five species distributed in Spain, Morocco, and Algeria. In his comprehensive revision of the tribe Brassiceae, Schulz (1923) placed *Boleum*, *Vella*, *Carrichtera* DC., *Psychine* Desfontaines, *Rytidocarpus* Cosson (as *Distomocarpus* O. E. Schulz), *Schouwia* DC., and *Succowia* Medikus in the subtribe Vellinae, and placed *Euzomodendron*, *Savignya* DC., and *Oudneya* R. Brown in the subtribe Savignyinae. Schulz (1919, 1936) separated these subtribes primarily on the basis of presence vs. absence of the median nectar glands and seed wing: the Vellinae have the median glands and lack the seed wing, whereas the Savignyinae lack the median nectar glands and have the seed wing. Gómez-Campo (1978), however, indicated the presence of vestigial wings in *Boleum* and *Vella* and suggested that *Euzomodendron* should be placed with these two genera in one group. He also suggested (Gómez-Campo, 1980) that the Savignyinae be united with the Vellinae.

Except for the shape of the valvular segment and the presence of a well-developed seed wing, *Euzomodendron* resembles *Vella* and *Boleum* in almost all other morphological characters, especially the woody habit, connation of inner filaments in pairs, and presence of short pedicels, saccate lateral sepals, long petal claws, dark-veined petal blades, seedless flattened beaks, strongly 3- or 5-veined valves, and acutely notched cotyledons (Table 1). In fact, Gómez-Campo (1978) indicated that "the robust valves [of *Euzomodendron*] with narrowed

base resemble that of *Vella*," and Gómez-Campo and Tortosa (1974) showed that the cotyledonary notch is indistinguishable in the three genera. However, not only did recent floristic accounts (e.g., Gómez-Campo, 1993; López-González, 1993; Marcos-Samaniego, 1993; Heywood, 1993) maintain the three genera but also placed *Euzomodendron* remotely from *Boleum* and *Vella*. These three genera have been maintained historically because of the taxonomic value placed on the fruit length, fruit dehiscence, and seed wing. In our opinion, the overwhelming similarities in all other characters have been either ignored or given insufficient weight. The connation of the inner filaments into pairs in *Euzomodendron*, *Boleum*, and *Vella* is a remarkable synapomorphy not found elsewhere in the tribe Brassiceae. Several large genera (e.g., *Draba* L., *Arabis* L., and *Erysimum* L.), and even a smaller one such as *Lobularia* Desvaux (4 spp.; Borgen, 1987), include taxa with winged or wingless seeds, whereas *Draba*, *Rorippa* Scopoli, and *Leavenworthia* Torrey, to name just a few, include species with both globose and narrowly oblong to linear fruits (for the many examples, see Rollins, 1993). Therefore, fruit shape and presence of the seed wing often do not warrant the delimitation of genera, especially when used alone.

The similarities between *Boleum* and *Vella* are even stronger than between these and *Euzomodendron*. The "most reliable" characters used to separate the first two are the presence in *Boleum* of short-pedicellate, indehiscent, sessile fruits, and in *Vella* of slightly longer-pedicelled, dehiscent, gynophorate or sessile fruits (Table 1). These characters do not justify the maintenance of these genera. In fact, dehiscent and indehiscent fruits can be found within *Tetracme* Bunge, *Coronopus* Zinn, *Sterigmostemum* M. Bieberstein, and *Ornithocarpa* Rose (or even on the same plant, as in *Diptychocarpus strictus* (DC.) Trautvetter, *Cardamine chen-*

Table 1. Comparison of *Boleum*, *Euzomodendron*, *Vella*, and *Carrichtera*.

Character/trait	<i>Boleum</i>	<i>Euzomodendron</i>	<i>Vella</i>	<i>Carrichtera</i>
Chromosome no.	$n = 51$	$n = 17$	$n = 17, 34$	$n = 8, 16$
Duration	perennial	perennial	perennial	annual
Habit	shrub	shrub	shrub	herb
Spines	absent	absent	present or absent	absent
Leaves	entire to few-lobed	pinnatisect or few-lobed	entire, few-lobed, or pinnatisect	1- or 2-pinnatisect
Inflorescence	many-flowered	many-flowered	few- or many-flowered	many-flowered
Flower pedicel	0.3–1(–2) mm	1–3 mm	0.5–2 mm	1–3 mm
Sepals lateral pair	saccate	saccate	saccate	slightly saccate
Petal length	11–16 mm	16–20 mm	(8–)10–20 mm	6–8 mm
Petal claw length	7–11 mm	10–12 mm	(6–)7–15 mm	3–4 mm
Petal blade color/veins	pale yellow/red-dish brown	cream/violet	yellow/violet or brown	pale yellow/violet
Filaments of inner stamens	united in pairs	united in pairs	united in pairs	free
Fruit gynophore	absent	absent	absent to 2 mm	absent
Fruit dehiscence	indehiscent	dehiscent	dehiscent	dehiscent
Valve venation	3-veined	3–5-veined	3–5-veined	3-veined
Valve pubescence	hispid	glabrous	hispid to glabrous	hispid
Valvular segment shape	globose or ellipsoid	linear	globose or ellipsoid	ellipsoid
Valvular segment length	3–4 mm	20–35 mm	4–6 mm	3–4 mm
Upper segment shape	lingulate	linear-lanceolate to oblong-triangular	lingulate, ensiform, or cochleariform	cochleariform
Upper segment length	4–7 mm	(3–)5–9(–11) mm	4–12(–15) mm	4–6 mm
Seeds per locule	1	6–8	1 (or 2)	2 or 3
Seed wing	vestigial	well developed	vestigial	absent
Cotyledons	acutely notched	acutely notched	acutely notched	acutely notched
Distribution	NE Spain (4 provinces)	SE Spain (Almeria Prov.)	Spain, Morocco, Algeria	SW Asia E to Iran and Mediterranean

opodiifolia Persoon, and several species of *Aethionema* R. Brown). Similarly, long-gynophorate or sessile fruits can be found in many genera, including *Brassica* L., *Romanschulzia* O. E. Schulz, *Thelypodium* Endlicher, and *Lunaria* L. (Rollins, 1993; Ball, 1993). Therefore, the characters used to distinguish *Boleum* from *Vella* are insufficient to maintain the two genera, and we believe that the two, along with *Euzomodendron*, form a well-defined natural group.

Results from a numerical study based on 32 morphometric characters (Gómez-Campo, 1981) did not support the separation of *Boleum* from *Vella* (*Euzomodendron* was not included in the study). *Boleum asperum* clustered within *Vella* and was closer to *V. anremerica* (Litardière & Maire) Gómez-Cam-

po and *V. mairei* Humbert than the latter two were to *V. spinosa* Boissier and *V. pseudocytisus* L.

Boleum ($n = 51$), *Vella* ($n = 17, 34$), and *Euzomodendron* ($n = 17$) share the same base chromosome number of $x = 17$, which is essentially unique in the tribe Brassiceae, with *Boleum asperum* representing a hexaploid derivative of this complex (Gómez-Campo, 1981; Gómez-Campo & Hinata, 1980; Warwick & Anderson, 1993). The only exception is *Brassica carinata* A. Braun ($n = 17$), the classical allotetraploid species derived from *B. oleracea* L. ($n = 9$) and *B. nigra* (L.) W. D. J. Koch ($n = 8$).

Boleum is restricted to northeastern Spain (Huesca, Lérida, Teruel, and Zaragoza provinces), whereas *Euzomodendron* is endemic to Almería

province in southeastern Spain. In contrast, the range of *Vella* occupies the area between the ranges of *Boleum* and *Euzomodendron* and extends southward into Morocco and adjacent Algeria. This complex occupies a distinct geographical area delimited by eastern and southern Spain into northwestern Africa. On the other hand, the single species of *Carrichtera*, *C. annua* (L.) DC., is a widespread circum-Mediterranean annual weed that extends eastward into Iran (Crespo, 1992; Gómez-Campo, 1993; Greuter et al., 1986; López-González, 1993; Maire, 1967; Marcos-Samaniego, 1993; Warwick & Francis, 1994).

Recent molecular studies of the chloroplast DNA restriction site variation of the three genera (Warwick & Black, 1994) also support the congeneric status of *Boleum*, *Euzomodendron*, and *Vella*. In their strict consensus tree, *V. spinosa*, *B. asperum*, *E. bourgaeum*, and *Vella anremerica* formed a well-supported clade that was observed in all 28 most parsimonious trees and 100% of the bootstrapping replicates. They showed that the latter clade was defined by 21 steps, compared, for example, to two steps for *Moricandia* and eight steps for *Zilla*. *Carrichtera annua* consistently formed a sister clade to the above four species in all the analyses. Within the *Vella-Boleum-Euzomodendron* clade, *V. anremerica* was placed as the sister group to the clade containing *Vella spinosa*, *Boleum*, and *Euzomodendron* in 21 of the 28 equally most parsimonious trees, whereas *Boleum* formed the sister clade in the seven remaining trees. In all the trees, however, the sister taxon to *Euzomodendron* was a species of *Vella*. These data show that both *Boleum* and *Euzomodendron* are nested within *Vella*. Similar results by Crespo et al. (1998), which are based on sequence data from the internal transcribed spacer region (ITS) of rDNA, indicate that both *Boleum* and *Euzomodendron* fall within *Vella*, with *Carrichtera* forming the sister clade. These molecular studies on totally different genomes provide convincing evidence that supports the reduction of *Boleum* and *Euzomodendron* to synonymy of the earlier published *Vella*.

Crespo et al.'s (1998) analysis of 23 morphological characters separately and in combination with the ITS data were consistent with the placement of *Boleum* with *Vella*. The combined analysis, however, showed *Euzomodendron* as a sister (basal) clade to that containing *Boleum* and the five *Vella* species (100% bootstrapping replicates), with *Carrichtera* forming the sister clade to the above group. Both molecular (Warwick & Black, 1994; Crespo et al., 1998) and morphological studies (Gómez-Campo, 1981; Crespo et al., 1998) support the inclusion

of *Boleum* in *Vella*. Similarly, both molecular data sets (Warwick & Black, 1994; Crespo et al., 1998) support the inclusion of *Euzomodendron* within *Vella*. The basal position of *Euzomodendron* in the combined morphological and molecular analysis of Crespo et al. (1998) is consistent with its more "primitive elongated fruits." However, we believe that the elongated vs. short fruits and well-developed vs. vestigial seed wing do not justify the recognition of *Euzomodendron* as a distinct genus. The unique chromosome number ($x = 17$) and connate filaments, which are restricted in the tribe Brassiceae to the *Boleum-Euzomodendron-Vella* complex, as well as the numerous similarities in morphology and geographic distribution, clearly are in full agreement with molecular data that the complex forms a well-defined genus.

The morphological, geographical, cytological, and molecular data are consistent with the recognition of *Carrichtera* as a separate genus from *Vella* (including *Boleum* and *Euzomodendron*). It resembles most taxa of *Vella* in having a cochleariform upper fruit segment, strongly veined valves, colored petal veins, dehiscent ellipsoid valvular fruit segments, and short pedicels. However, *Carrichtera* differs in being an annual herb with free inner filaments, and much shorter (3–4 vs. 7–15 mm) petal claws. The distinct generic status of *Carrichtera* is also supported by differences in chloroplast DNA restriction site data (Warwick & Black, 1994), ITS sequence data (Crespo et al., 1998), and chromosome numbers (Gómez-Campo & Hinata, 1980; Warwick & Anderson, 1993).

The limits of *Vella* are expanded here to include both *Boleum* and *Euzomodendron*. The combined genus consists of seven species, and names for all except one are available in *Vella*.

Vella L., Sp. Pl. 2: 641. 1753. TYPE: *Vella pseudocytisus* L.

Boleum Desvaux, J. Bot. 3: 163. 1815. Syn. nov. TYPE: *Boleum asperum* (Persoon) Desvaux.

Euzomodendron Cosson, Notes Pl. Crit. 144. 1852. Syn. nov. TYPE: *Euzomodendron bourgaeum* Cosson.

Shrubs to 1 m tall, spiny or unarmed, sparsely to densely hairy to setose. Leaves entire to pinnatisect, sessile to short petiolate. Inflorescences ebracteate, few- to many-flowered racemes; flowering pedicels obsolete to short, rarely to 3 mm in fruit. Sepals erect, lateral pair saccate at base. Petals yellow, pale yellow, or cream, with reddish brown or violet veins; claw slender, much longer than sepals. Stamens tetradynamous; inner filaments united in pairs. Lateral nectar glands 2-

lobed to prismatic or semi-annular; median glands present or absent. Style as long as ovary or shorter; stigma capitate. Fruits 2-segmented, sessile or on a gynophore to 2 mm; valvular segment globose to ellipsoid or linear-lanceolate, 1–8-seeded per locule, dehiscent or rarely indehiscent; valves strongly 3- or 5-veined, hispid to setiform or rarely glabrous; septum complete; upper segment lingulate to ensiform or cochleariform, seedless. Seeds with a vestigial wing, rarely winged all around; cotyledons conduplicate. Chromosome number: $x = 17$.

- 1a. Plants spiny, inflorescences few-flowered.
- 2a. Fruits hairy, upper segment 12–15 mm long; leaves usually pinnatisect or several-lobed, apex obtuse *V. mairei* Humbert
- 2b. Fruits glabrous, upper segment 6–7 mm long; leaves usually entire, rarely 1- or 2-lobed, apex acute *V. spinosa* Boissier
- 1b. Plants not spiny, inflorescences many-flowered.
- 3a. Valvular fruit segment linear-lanceolate, 20–35 mm long; seeds distinctly winged all around . . . *V. bourgaeana* (Cosson) Warwick & Al-Shehbaz
- 3b. Valvular fruit segment globose or ellipsoid, 3–6 mm long; seeds with a vestigial wing.
- 4a. Leaf apex obtuse to rounded; upper fruit segment cochleariform *V. pseudocytisus* L.
- 4b. Leaf apex acute to acuminate; upper fruit segment lingulate.
- 5a. Leaves and sepals appressed hairy; plants of Morocco *V. anremerica* (Litardière & Maire) Gómez-Campo
- 5b. Leaves and sepals spreading hairy or setose; plants of Spain.
- 6a. Leaves linear, to 2 mm wide, entire; fruit on a gynophore ca. 1 mm long, lower segment dehiscent *V. lucentina* M. B. Crespo
- 6b. Leaves linear lanceolate, 2–4.5 mm wide usually with 1 or 2 pairs of lateral lobes, rarely entire; fruit sessile, lower segment indehiscent *V. aspera* Persoon

Vella bourgaeana (Cosson) Warwick & Al-Shehbaz, comb. nov. Basionym: *Euzomodendron bourgaeum* Cosson, Notes Pl. Crit. 145. 1852. TYPE: Spain. "In calcareis salsuginosis Hispaniae orientalis australioris, in ditone Almeriensi ad basim montis Sierra de Gador inter oppida Santa Fe et Huesica," 6 June 1851, *E. Bourgeau 1055* (holotype, P).

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Literature Cited

- Ball, P. W. 1993. *Lunaria*. In: T. G. Tutin et al. (editors), *Flora Europaea*, ed. 2, 1: 358. Cambridge Univ. Press, Cambridge (U.K.).
- Borgen, L. 1987. *Lobularia* (Cruciferae), a biosystematic study with special reference to the Macaronesian region. *Opera Bot.* 91: 1–96.
- Crespo, M. B. 1992. A new species of *Vella* L. (Brassicaceae) from the south-eastern part of the Iberian Peninsula. *Bot. J. Linn. Soc.* 109: 369–376.
- , M. D. Lledó, M. F. Fay & M. W. Chase. 1998. Subtribe Vellinae (Brassicaceae, Brassicaceae): A combined analysis of ITS rDNA sequences and morphological data. *Amer. J. Bot.* (in press).
- Gómez-Campo, C. 1978. Studies on Cruciferae: VI. Geographical distribution and conservation status of *Boleum* Desv., *Guiraoa* Coss. and *Euzomodendron* Coss. *Anal. Inst. Bot. Cavanilles* 35: 165–176.
- . 1980. Morphology and morpho-taxonomy of the tribe Brassiceae. Pp. 3–31 in S. Tsunoda, K. Hinata & C. Gómez-Campo (editors), *Brassica Crops and Wild Allies*. Japan Science Societies Press, Tokyo.
- . 1981. Taxonomic and evolutionary relationships in the genus *Vella* L. (Cruciferae). *Bot. J. Linn. Soc.* 82: 165–179.
- . 1993. *Vella*. In: S. Castroviejo et al. (editors), *Flora Iberica* 4: 414–417. Real Jardín Botánico, Madrid.
- & K. Hinata. 1980. A check list of chromosome numbers in the tribe Brassiceae. Pp. 51–63 in S. Tsunoda, K. Hinata & C. Gómez-Campo (editors), *Brassica Crops and Wild Allies*. Japan Science Societies Press, Tokyo.
- & M. E. Tortosa. 1974. The taxonomic and evolutionary significance of some juvenile characters in the Brassiceae. *Bot. J. Linn. Soc.* 69: 105–124.
- Greuter, W., H. M. Burdet & G. Long (Editors). 1986. *Cruciferae*. Med-checklist 3: 34–172. Conservatoire et Jardin Botaniques de la Ville de Genève, OPTIMA, Genève.
- Heywood, V. H. 1993. *Euzomodendron*, *Vella*, and *Boleum*. In: T. G. Tutin et al. (editors), *Flora Europaea*, ed. 2, 1: 403–404, 413. Cambridge Univ. Press, Cambridge (U.K.).
- López-González, G. 1993. *Euzomodendron*. In: S. Castroviejo et al. (editors), *Flora Iberica* 4: 344–346. Real Jardín Botánico, Madrid.
- Maire, R. 1967. Flore de l'Afrique du Nord. 13: 1–365. Paul Lechevalier, Paris.
- Marcos-Samaniego, N. 1993. *Boleum*. In: S. Castroviejo et al. (editors), *Flora Iberica* 4: 419–421. Real Jardín Botánico, Madrid.
- Rollins, R. C. 1993. The Cruciferae of Continental North America. Stanford Univ. Press, Stanford.
- Schulz, O. E. 1919. Cruciferae–Brassicaceae. Part 1. In: A. Engler (editor), *Pflanzenr.* IV. 105(Heft 70): 1–290.
- . 1923. IV. 105. Cruciferae–Brassicaceae. Part 2. In: A. Engler (editor), *Pflanzenr.* IV. 105(Heft 84): 1–100.
- . 1936. Cruciferae. In: A. Engler & K. Prantl (editors), *Natürlichen Pflanzenfamilien* ed. 2, 17B: 227–658.
- Warwick, S. I. & J. K. Anderson. 1993. Guide to the wild germplasm of *Brassica* and allied crops. Part II. Chromosome numbers in the tribe Brassiceae (Cruciferae). *Agriculture Canada Res. Branch Tech. Bull.* 1993-15E.
- & L. D. Black. 1994. Evaluation of the subtribes

Moricandiinae, Savignyinae, Vellinae and Zillinae (Brassicaceae, tribe Brassiceae) using chloroplast DNA restriction site variation. *Canad. J. Bot.* 72: 1692–1701.
——— & A. Francis. 1994. Guide to the wild germplasm

of *Brassica* and allied crops. Part V. Life history and geographical data for wild species in the tribe Brassiceae (Cruciferae). Agriculture Canada Res. Branch Tech. Bull. 1994-2E.